# Rites of Passage: Germination of Vertebrate Dispersed, Regurgitated or Defecated *Phoenix canariensis* Seeds

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Published on 22 October at https://openjournals.library.sydney.edu.au/index.php/LIN/index

Spennemann, D.H.R. and Pike, M. (2019). Rites of passage: germination of vertebrate dispersed, regurgitated or defecated *Phoenix canariensis* seeds. *Proceedings of the Linnean Society of New South Wales* **141**: 49-58.

Canary Island Date Palms are widely planted as ornamental plants in private and public spaces. As both prolific and long-duration seeders, their drupes provide food for a range of volant and terrestrial vertebrates. This study experimentally examined the germination of vertebrate digested seeds. Whereas seeds in Flying-fox spat did not yield a higher germination rate than undigested controls, seeds that had passed through the gastro-intestinal tract and were deposited in scats, or those that were ingested and regurgitated from the crop, have a significantly better probability of germinating. This establishes Pied Currawongs as effective short-range dispersers and canid frugivores, such as the Red Fox, as major medium- and long-distance vectors of ornamental palms.

Manuscript received 8 March 2019, accepted for publication 9 October 2019.

KEYWORDS: invasive species, frugivory, palmae, seed dispersal; Strepera graculina, Vulpes vulpes.

# INTRODUCTION

The seeds of many plants are dispersed via the gastro-intestinal tract of volant and terrestrial vertebrates (Corlett 1998; Corlett 2017; Fedriani and Delibes 2009; Levey, Silva and Galetti 2002; Tsuji, Morimoto and Matsubayashi 2009). Palms are no different in that regard (Zona and Henderson 1989). In addition, studies have shown that some plants benefit from ingestion as mastication and digestive action, as well as immersion in gastric and intestinal fluids, scarifies the seed coat aiding germination (Colon and Campos-Arceiz 2013; Reid and Armesto 2011; Rodriguez-Perez, Riera and Traveset 2005; Traveset 1998).

While a number of volant and terrestrial species are documented as vectors of Canary Island Date Palms (*Phoenix canariensis*) and their congeners (Spennemann 2018f; Zona and Henderson 1989), and thus contribute to the plants' invasiveness, there is a lack of experimental studies that assesses the germination potential of vertebrate dispersed seeds compared with naturally abscised seeds.

A study into the spread of horticulturallyplanted Canary Island Date Palms into an agricultural landscape in south-eastern Australia yielded a number of vertebrate dispersed seeds extracted from scats and regurgitates, which allowed for an experimental examination of the issue.

# BACKGROUND

#### Phoenix canariensis

Phoenix canariensis H.Wildpret ex Chabaud (Arecaceae) is a dioecious anemophilous plant that is solely propagated by seed (Barrow 1998), with pollination occurring at distances in excess of 390m (Saro, Robledo-Arnuncio, González-Pérez and Sosa 2014). Canary Island Date Palm readily and reliably sets fruit and seeds freely, annually producing between 5,000 and 30,000 obovoid drupes ('dates') (Djouab, Benamara, Gougam, Amellal and Hidous 2016; Saro et al. 2014), which are a fleshy fruit with a small, single seed and small amount of fibrous pericarp. The drupes range from 15-30mm in length, 12-17mm in

thickness and 2–5g in mass (Djouab et al. 2016), of which the seed contributes between 0.9–1.5g. The drupes, which occur in hanging clusters, vary widely in their physical properties (shape, length, diameter, mass, colour) between individual palms. When ripe, they attain a dark orange to red colour.

The Canary Island Date Palm reaches reproductive maturity and first flowers after six to seven years (in some locales between 8 to 10 years)(Borzì 1912), which is the first time that a plant's gender can be determined. In the southern hemisphere P. canariensis drupes ripen between March and June (northern hemisphere: November and February), with fruit available to birds until late November (pers. obs.) (Núñez 1997:82). Immediately following ripening, the germination rate of P. canariensis is very high (~93%) (Noto and Romano 1987). The seed, which requires temperatures between 25°C and 35°C to germinate (Chatty and Tissaoui 1999; Pimenta, da Luz, Pivetta, de Castro and Pizetta 2010) shows its first two-leave shoots at about one year of age (Borzì 1912; Noto and Romano 1987).

Unless affected by disease or pests, the plant can live for 200-300 years (Beech 2017). In its natural distribution, *P. canariensis* is endemic to the Canary Islands (Lipnitz and Kretschmar 1994; Sosa, Naranjo, Márquez, Gil and Saro 2016). It was quickly and widely dispersed during the second half of the ninetieth century as a horticultural feature plant and street tree (Spennemann 2018a; Spennemann 2019b; Zona 2008). Today it is distributed globally in all warm temperate regions (Spennemann 2018b).

As the plants seed freely and their fruits ('drupes') are consumed by a number of vectors, P. canariensis has become a weed species that is known to colonise and invade natural areas. In various Australian states. P. canariensis it is widely referred to as a 'nuisance plant' (Ku-ring-gai Council 2007:20), 'a garden escape taking up much time to control' (Gye and Thomas 2007), a 'species with huge potential as an invasive weed' (Anonymous 2016) or is even listed 'among the ten worst environmental weeds' (Landcare Echuca 2013). Richardson et al. noted it as a weed plant that "has started to establish along waterways across the regions (NSW, Vic, SA, WA)" (Richardson, Richardson and Shepherd 2006:13f; Richardson, Richardson and Shepherd 2011:19f). In the Australasian setting, P. canariensis have been formally regarded as naturalised in New South Wales (Hosking, Conn, Lepschi and Barker 2007), South Australia (Brodie and Reynolds 2012), south-eastern Queensland (Biosecurity Queensland 2018), Victoria (Conn and Walsh 1993), and Western Australia (Lohr and Keighery 2016:32), as well as Norfolk Island

(Biosecurity Queensland 2018) and New Zealand (Esler 1987).

#### Vectors

The primary, long-distance dispersal agent for P. canariensis are people, in particular when planting specimens of the palm species as ornamentals (Spennemann 2018a; Spennemann 2018c; Zona 2008). Globally, a range of volant and terrestrial vertebrate vectors are responsible for the dispersal of P. canariensis (Spennemann 2019c). Given the size of the seed (8.8-12.2 mm diameter) (Spennemann 2019d), in the Australian context fruit bats (such as Pteropus poliocephalus) are possible (Augee and Parry-Jones 1991; Parry-Jones and Augee 1991), but less common dispersers (Spennemann 2018d). The gape size of birds determines their ability to swallow and disperse seeds (Lord 2004; Rey and Gutierrez 1996; Wheelwright 1985). In the Australian context dispersers these are primarily Blackbirds (Turdus merula) dispersing to the closest cover (pers. obs.) and Pied Currawong (Strepera graculina) predominantly dispersing to the closest perch (Bass 1995). A major consumer of abscised drupes are canids such as the Red Fox (Vulpes vulpes), which can transport seeds in their gastro-intestinal tract over greater distances (Debussche and Isenmann 1989; Szuman and Skrzydlewski 1962). The defecation occurs gradually. Field trials suggest that the Red Fox defecates five times in a 24-hour period (Ryszkowski et al. cited after Sequeira 1980). Their behaviour of territorial scent marking results in defecation on or near the same spots, leading to accumulation of scats (Spennemann 2018e) and thus an increased potential for germination.

# **Germination Studies**

A plethora of papers exist that comment on the germination of palm seeds in general (Baskin and Baskin 2014; Broschat and Donselman 1989; Chatty and Tissaoui 1999; Donselman 1982; Gátin 1906; Marcus and Banks 1999; Meerow and Broschat 2017; Mifsud 1996; Pritchard, Wood, Hodges and Vautier 2004; Robinson 2009), as well as on the germination on the congener of *P. canariensis*, the commercially grown date palm *P. dactylifera* (Azad, Rahman and Matin 2011; Singh and Bhargava 2009; Sumianah, Makki and Rumney 1984). Only two studies refer specifically to *P. canariensis* (El-Tarawy, Menesy and Nofal 1989; Pimenta et al. 2010).

There is only a limited number of papers on the germination of vertebrate-ingested palm seed, all relating to seed consumed by coyotes (*Canis latrans*) and racoons (*Procyonlotor*). Studies of the germination



Figure 1. Excreta of the Red Fox (Glenalvon palm n° 7). Sample APV6.

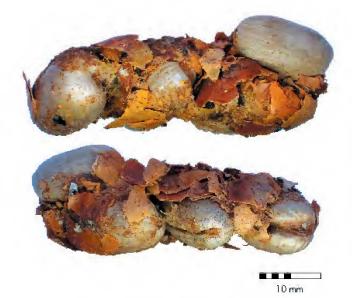


Figure 2. Pellet of undigested material regurgitated by a Pied Currawong (Lieschke palm n° 16). Sample APS24.

of *Washingtonia filifera* seeds ingested by coyotes and racoons provided no or only limited guidance on an appropriate, and replicable methodology (Bullock 1980; Cornett 1985; Cypher and Cypher 1999; Silverstein 2005). Silverstein's (2005) paper is the only study that examined the germination of *Phoenix* spp. seeds after ingestion by vertebrates.

He obtained Phoenix spp. (and Washingtonia) seeds coyote scats and planted them in a seed starter potting soil in compartmentalized plastic growing trays which were placed in various outdoor and indoor locations. Some of the seeds were pre-treated by washing them for 30 seconds in a 5% bleach solution. Silverstein found that 46.7% of the *Phoenix* seeds (n=60) germinated with a mean of 95 days to germination, whereas W. filifera had a germination rate of 75.8% (mean of 71 days) (Silverstein 2005).

# MATERIALS AND METHODS

# The origin of the samples

The P, canariensis seeds used for the experiment were extracted from fox scats (Figure 1), Currawong regurgitates (Figure 2) and flying fox spats collected at the Lutheran Church as well as the property 'Glenalvon' at Alma Park, NSW (Spennemann 2018e). As controls, abscised clean seeds as well as abscised seeds with adhering flesh were collected under palm 15 at 'Glenalvon,' Alma Park. The Alma Park location has been used for a number of studies relating to P. canariensis.

# Design

The basic methodology used for the experiments reported here followed that of Pimenta et al. (2010). It comprised a regime of 16 hours

of simulated daylight and 8 hours of darkness and with environmental temperatures fluctuating between 20°C during the 'night' and 30°C during the 'day.'

The experiment was set up in a climate controlled, window-less laboratory room of 2.6 x 2.8 m. Light was provided by three AquaOne® EcoGlo90 LED lights,

caperiment									
Туре	Location	2 weeks	3 weeks	4 weeks	5 weeks	n			
Currawong	Church	67.52	79.62	80.25	80.25	157			
Flying-fox	Glenalvon	50.00	50.00	50.00	50.00	12			
Fox	Glenalvon	78.57	88.10	88.10	88.10	84			
Abscised seed (2017 season)	Glenalvon	12.00	32.00	48.00	52.00	25			
Abscised seed (2018 season)	Glenalvon	38.46	53.85	57.69	57.69	26			

Table 1. Percentage of seeds germinating at Alma Park: Natural soil conditions experiment

each set up centrally above a plastic container. These lights primarily emit at the 430–490 nm spectrum (blue light) and 420–780nm spectrum (white light, peaks at 460nm and 540–620nm). A stable ambient temperature was achieved by the room-specific airconditioning system, which was manually adjusted twice a day. The temperature was set at the start of the simulated 'day' to 30°C (17:00–9:00) and left cool at the end of the 'day' with the 'night' (9:00–17:00) set at a stable 20°C. Given the small air space, both the drop and rise of ambient temperature were rapid. Actual room temperatures were logged with a TinyTag Plus 2 TGP-4500 temperature and humidity logger.

The results were analysed in MS Excel and compared with the Chi-squared test with n-1 correction (Campbell 2007; MedCalc Software 2018; Richardson 2011).

#### **Natural soil conditions experiment (A)**

To replicate natural germination conditions to the extent possible, the samples were housed in three transparent plastic tubs with lids (34 l, 390 x 790 x 155mm), each filled with 13.331 of evenly mixed planting substrate comprised of 50% peat moss and 50% Perlite. The surface was levelled and divided into a 3 x 6 grid using wooden skewers. Each cell was populated with nine seeds (3 x 3 pattern). The seeds had been cleaned of adhering material (if any) and measured prior to the experiment (see above). No fungicides were applied in order to simulate natural conditions. The seeds were pressed into substrate. level with the surface, and with their operculum pointing upwards. The surface was then moistened with 1.351 of standard tap water sprayed with a pressurised mist sprayer evenly across the surface of the tub. The lids were then replaced for the first 48hrs, after which they were removed. This experiment was carried out between 14 June and 27 July 2018. The total number of seeds pertinent to this paper are set out in Table 1.

# Soaked seeds experiment (B)

Numerous advice pages on palm seed germination recommend to place seeds between a peatmoss and vermiculite mixture placed in sealed plastic bags or merely between moist paper tissues in sealed plastic bags which are then placed in a warm space (Marcus and Banks 1999; Spanner 2018). The latter method was employed in order to test the germination success of this seasons seeds compared to last season's seeds and to assess the effect of soaking on larger samples. In addition to these primary samples, a number of seeds regurgitated by Currawongs were added.

One half of the samples was pre-treated by soaking the seeds in tap water for 24hrs, while the other half remained untreated. As before, no fungicides were applied in order to simulate natural conditions. The bags were opened after two weeks to assess the rate of germination. All germinated seeds were removed, the bags remoistened and resealed for another week. This process was repeated twice after which the experiment was terminated. The experiment was carried out between 21 June and 20 July 2018. The total number of seeds pertinent to this paper are set out in Table 3.

# Recording of germination

In all experiments, the emergence of the cotyledonary petiole (often mistakenly called the radicle) from the operculum was taken as successful germination (Pimenta et al. 2010).

# **RESULTS**

The percentage of animal dispersed seed germination reached its maximum after three weeks, whereas non-ingested seeds continued to germinate in the weeks after that (Table 1; 2). The highest rate of germination was observed for *P. canariensis* seed in fox scats (88.1%) followed by Currawongs (80.3%) and the controls. The germination rate of seeds

Treatment	Туре	Location	2 weeks	3 weeks	4 weeks	5 weeks	n	
not	Currawong	Alma Park Church	72.7	72.7	72.7	J.	66	χ²= 46.941;
soaked	Abscised seed	Alma Park Glenalvon	16.5	19.3	20.2	./.	109	p< 0.0001
	rodent eaten	Alma Park D14	0.0	0.0	0.0	./.	18	
soaked	Currawong	Alma Park Church	71.2	72.7	72.7	./.	66	$\chi^2 = 16.275;$
	Abscised	Alma Park Glonalyon	20.2	/1 1	/1 1	,	107	p = 0.0001

38.3

41.1

Table 2. Percentage of seeds germinating: Soaked seeds experiment

Alma Park Glenalyon

seed



Figure 3. Phoenix canariensis seed gnawed by a small rodent (D14).

recovered from Flying-fox spats was 50%, while, not surprisingly, none of the rodent-bitten seeds (Figure 3) germinated.

The natural soil conditions experiment found that the observed germination rate for seeds in fox scats and Currawong regurgitates was significantly better than that for and the undigested abscised control seeds (Table 2). There was, however, no statistical difference between the germination rate of seeds in Flying-fox spats and undigested abscised controls (Table 3).

# DISCUSSION

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While vertebrates prime dispersers of palm seeds, their effectiveness varies. The comparatively low level of germination success of seeds in Flying-fox spats can be interpreted as the result of a complete lack of scarification. The mastication action of the animal will either tear the pericarp off the seed, leaving striations (Figure 4) or will chew the whole drupe, separating the pericarp from the seed in the oral cavity (Spennemann 2018d). The seed itself is not subjected to any further physical impact, but is pushed to the front of the mouth and ejected with masticated epicarp platelets and squeezed-out endocarp fibres. The observation that the germination rate among Flying-fox dispersed seeds is less than that of the controls could be explained by the fact that the controls lying on the ground had been exposed to some modicum of photo-chemical erosion. As the majority of spit-outs occur at the

source tree, Flying-foxes provide very little dispersal benefits.

Even though only a small percentage of volant vectors ingest drupes, birds are by far the most significant in terms of pure quantities of seeds dispersed (in litt.). The size of the seeds that can be dispersed is regulated by the bird's gape size, whereas the overall size of the bird and its crop determines the quantity of seed that can be consumed and thus dispersed. The majority of birds, such as Currawongs, tend to fly to the closest perch to digest their food. There the seeds

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Table 3. Differences between the germination rates of vertebrate dispersed seed and controls (naturally abscised seed), Natural soil conditions experiment

				abscised seeds		
	Fox	Currawong	Flying Fox	2017 season	2018 season	
Fox	_	χ2=2.378; p=0.1230	χ2=10.862; p=0.0010	χ2=15.445; p=0.0001	χ2= 11.780; p=0.0006	
Currawong	_	_	χ2=6.351; p=0.0117	χ2=9.485; p=0.0021	χ2=6.384; p=0.0115	



Figure 4. P. canariensis seed chewed by a Flying-fox.

are regurgitated after less than 20 minutes (Bass 1995). Even though large quantities of seeds accumulate under these perches, their residence time in the bird's gizzard is only very short. Albeit short, the residence time, coupled with the abrading action in the gizzard is sufficient to significantly increase the germination potential compared to naturally abscised seed. Thus the main benefit of Currawongs as vectors rests in the albeit short-distance spatial dispersal of seeds, the quantity of seeds deposited at given locations and the improved germination potential. The net benefit to the palm is less an increase in spatial distribution, but an intensification of its coverage. Dispersal over greater distances occurs only when Currawongs return to their night roosts (Bass 1995).

These findings cannot be extrapolated for smaller birds, such as Blackbirds (*Turdus merula*), Starlings (*Sturnus vulgaris*) and Common Myna (*Sturnus [Acridotheres] tristis*), all of which are known dispersers (Spennemann 2019c), but which have both a smaller gizzard and shorter residence times for ingested fruit.

Canids are major dispersers of fruit including palm drupes (Graae. and Bruun 2004; Pagh Rico-Guzmán, Terrones, Cantó and Bonet 2012; Schmelitschek. French and Parry-Jones 2009; Spennemann and Allen 2000). In most instances the consumption of fruit and subsequent defecation of seed improves a seed's chances or germination success (Traba, Sagrario, Herranz and Clamagirand 2006; Varela and Bucher 2006). even though exceptions are on record (Morales-Paredes, Valdivia

and Sade 2015). The findings of this study of enhanced germination capacity conform with the majority of observations.

While vertebrate-dispersed seeds have a greater chance of germination, there are a number of factors post-dispersal that affect germination success, namely infestation by insects, predation by rodents and environmental factors. Seeds that successfully germinate while lying on the ground are on occasion lifted above the surface by their emergent radicles (Spennemann, Kent and Cook 2018:9), thus exposing the radicle to consumption by small rodents as well as to desiccation during warm weather events. It is not uncommon to find dry seed with open opercula under palms (pers. obs.). P. canariensis seeds under the source palms have a high chance of being predated by rodents (Figure 3), or becoming infested by date stone beetles (Coccotrypes dactyliperda) (Spennemann 2019a) which reduces a seed's ability to germinate and successfully develop into a small seedling. Seeds dispersed in canid faeces, however, tend to be avoided

by these beetles (Spennemann in press) and thus have a greater chance of establishment. Furthermore, as the germinating seeds are embedded in the matrix of the scats, they are less likely to be raised by the emerging radicle, and thus further protected from predation.

# **IMPLICATIONS**

In the Australian setting, the findings of this study establish the Red Fox as the main long-distance seed vector for Canary Island Date Palm seeds, not only in terms of dispersal distance and dispersal intensity due to repeated defecation at the same location in consequence of territorial scent marking (Gese and Ruff 1997; Macdonald 1979), but also in terms of dispersal success due to the high germination success and low level of post-depositional predation by seed boring beetles. Significantly, Red Foxes are also instrumental in the establishment of Canary Island Date Palms in spaces lacking perch trees, such as in (ungrazed) grassland and scrublands (see example in Spennemann 2018g). Only in areas where the Red Fox is less common, such as in inner urban areas (White, Gubiani, Smallman, Snell and Morton 2006), does dispersal by volant vectors appear to gain greater significance. Among these, Pied Currawong are an effective major vector due to their revisitation of preferred perches.

It would be beneficial to examine the germination potential of Canary Island Date Palm seeds regurgitated by smaller vectors, such as Blackbirds, Starlings and Common Myna. Given the difficulty of identifying and obtaining sufficient quantities of seeds regurgitated by these species, captive feeding experiments may be required.

# ACKNOWLEDGMENTS

We are indebted to Robert Cook and Kylie Kent (both Southern Area Technical Support Faculty of Science, Charles Sturt University) for assistance with the germination experiments. Dale Lieschke ('Glenalvon,' Alma Park, NSW) kindly permitted access to the palms on his property.

# REFERENCES

- Anonymous. (2016). Wednesday walk report 27/4/2016 House Creek in Gerard Moylan and Willows Park. Wodonga: Wodonga urban landcare network.
- Augee, M.L., Parry-Jones, K.A. (1991). The diet of flyingfoxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. Australian Zoologist 27, 49–54.

- Azad, M.S., Rahman, M.T., Matin, M.A. (2011). Seed germination techniques of Phoenix dactylifera: A new experience from Bangladesh. Frontiers of Agriculture in China 5, 241-246.
- Barrow, S.C. (1998). A monograph of *Phoenix L.* (Palmae: Coryphoideae). *Kew Bulletin* **53**, 513–575.
- Baskin, J.M., Baskin, C.C. (2014). What kind of seed dormancy might palms have? Seed Science Research 24, 17–22.
- Bass, D.A. (1995). Contribution of introduced fruits to the winter diet of Pied Currawongs in Armidale, New South Wales. Corella 19, 127-131.
- Beech, E. (2017). *Phoenix canariensis*, Palma Canaria. *The IUCN Red List of Threatened Species 2017*.
- Biosecurity Queensland. (2018). Phoenix canariensis hort. ex Chabaud Weeds of Australia Biosecurity Queensland Edition. Brisbane: Biosecurity Queensland, Queensland Government.
- Borzì, A. (1912). Sulla coltura del Dattero come Pianta da frutta in Sicilia. Bollettino dell R. Orto Botanico e Giardino Coloniale di Palermo 9, 40-60.
- Brodie, C., Reynolds, T. (2012). Review of recent plant naturalisations in South Australia and initial screening for weed risk Department for Environment and Natural Resources Technical Report 2012/02. Adelaide: Department for Environment and Natural Resources.
- Broschat, T.K., Donselman, H. (1989). Palm seed storage and germination studies. *Principes* 32, 3–12.
- Bullock, S.H. (1980). Dispersal of a desert palm by opportunistic frugivores. *Principes* 24, 29–32.
- Campbell, I. (2007). Chi-squared and Fisher-Irwin tests of two-by-two tables with small sample recommendations. Statistics in Medicine 26, 3661-3675.
- Chatty, Y., Tissaoui, T. (Year) of Conference. Effect of Temperature on Germination of Ornamental Palm Trees in Tunisia. II International Symposium on Ornamental Palms & other Monocots from the Tropics: ISHS Acta Horticulturae 486, 165–167.
- Colon, C.P., Campos-Arceiz, A. (2013). The impact of gut-passage by binturongs (*Arctictis binturong*) on seed germination. Raffles Bulletin of Zoology 61, 417-421.
- Conn, B., Walsh, N. (1993). Arecaceae. In: Walsh N and Entwistle T, eds. Flora of Victoria. Inkata Press: Melbourne. 165–167.
- Corlett, R.T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73, 413–448.
- Corlett, R.T. (2017). Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update *Global Ecology and Conservation* 11, 1–22.
- Cornett, J.W. (1985). Germination of Washingtonia filifera seeds eaten by coyotes. Principes 20, 19.
- Cypher, B.L., Cypher, E.A. (1999). Germination rates of tree seeds ingested by coyotes and raccoons. *The American Midland Naturalist* 142, 71-76.
- Debussche, M., Isenmann, P. (1989). Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikas* **56**, 327-338.
- Djouab, A., Benamara, S., Gougam, H., Amellal, H., Hidous, K. (2016). Physical and antioxidant properties of

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- two Algerian date fruit species (*Phoenix dactylifera L.* and *Phoenix canariensis L.*). Emirates Journal of Food and Agriculture **28**, 601-608.
- Donselman, H. (1982). Palm Seed Germination Studies. Proceedings of the Florida State Horticultural Society 95, 256–257.
- El-Tarawy, M.A., Menesy, F.A., Nofal, E.M. (1989). Seed germination and seedling growth of Canary Island date palm (Phoenix canariensis Chaub.) as affected by some pregermination treatments. *Journal of Agricultural* Research, Tanta University 13, 28–37.
- Esler, A.E. (1987). The naturalisation of plants in urban Auckland, New Zealand 2. Records of introduction and naturalisation. New Zealand Journal of Botany 25, 523-537.
- Fedriani, J.M., Delibes, M. (2009). Functional diversity in fruit-frugivore interactions: a field experiment with Mediterranean mammals. *Ecography* 32, 983-992.
- Gátin, C.-L. (1906). Recherches anatomiques et chimiques sur la germination des palmiers. Annales des sciences naturelles. Botanique 3, 191–314.
- Gese, E.M., Ruff, R.L. (1997). Scent-marking by coyotes, Canis latrans: the influence of social and ecological factors. Animal Behaviour 54, 1155-1166.
- Graae, B.J., Pagh, S., Bruun, H.H. (2004). An experimental evaluation of the Arctic fox (Alopex lagopus) as a seed disperser. Arctic, Antarctic, and Alpine Research 36, 468-473.
- Gye, J., Thomas, R. (2007). Paying the price of garden escapes. A snapshot of the work of bush regenerators and the weeds they encounter in Eastern Australia. Sydney South, NSW: Australian Association of Bush Regenerators.
- Hosking, J.R., Conn, B.J., Lepschi, B.J., Barker, C.H. (2007). Plant species first recognised as naturalised for New South Wales in 2002 and 2003, with additional comments on species recognised as naturalised in 2000–2001. Cunninghamia 10, 139–166.
- Ku-ring-gai Council. (2007). Weed Management Policy7. revised ed. ed. Gordon: Ku-ring-gai Council.
- Landcare Echuca. (2013). Environmental Weeds Problem plants of our district: Landcare Echuca.
- Levey, D.J., Silva, W.R., Galetti, M. (2002). Seed dispersal and frugivery: ecology, evolution and conservation. CABI International: Wallingford.
- Lipnitz, D., Kretschmar, M. (1994). Standortökologische Untersuchungen an *Phoenix canariensis* hort. ex Chabaud (Arecaceae) auf Gran Canaria und Teneriffa (Kanarische Inseln). *Palmarum Hortus Francofortensis:* Palmengarten wissenschaftliche Berichte 4, 23-63.
- Lohr, M.T., Keighery, G.J. (2016). The status and distribution of naturalised alien plants on the islands of the west coast of Western Australia. Conservation Science of Western Australia 10, 1–43.
- Lord, J.M. (2004). Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. Austral Ecology 29, 430-436.
- Macdonald, D.W. (1979). The flexible social system of the golden jackal, *Canis aureus. Behavioral Ecology and Sociobiology* 5, 17-38.

- Marcus, J., Banks, K. (1999). A Practical Guide to Germinating Palm Seeds. *Principes* **43**, 56-59.
- MedCalc Software. (2018). MEDCALC. Comparison of proportions calculator. Ostend: MedCalc Software.
- Meerow, A.W., Broschat, T.K. (2017). Palm Seed Germination. Miami: Environmental Horticulture Department UF/IFAS Extension.
- Mifsud, S. (1996). Germinating Palm Seeds. Chamaerops 23.

  Morales-Paredes, C., Valdivia, C.E., Sade, S. (2015). La

  frugivori□ a por ca□ nidos nativos (Lycalopex spp.)

  y alo□ ctonos (Canis lupus familiaris) reduce la

  germinacio□ n de semillas de litre (Lithrea caustica) en

  Chile central. Bosque (Valdivia) 36, 481-486.
- Noto, G., Romano, D. (1987). Palms in the Urban Environment in the Southern Latitudes of Italy. In: Thoday PR and Robinson DW, eds. The Scientific Management of Vegetation in the Urban Environment.: Acta Horticulturae. 91-97.
- Núñez, D.R. (1997). Frutos secos, oleaginosos, frutales de hueso, almendros y frutales de pepita. Editum.
- Parry-Jones, K.A., Augee, M.L. (1991). Food Selection by Grey-headed Flying Foxes (Pteropus poliocephalus) occupying a Summer Colony Site near Gosford, New South Wales. Wildlife Research 18, 111-124.
- Pimenta, R.S., da Luz, P.B., Pivetta, K.F.L., de Castro, A., Pizetta, P.U.C.s. (2010). Efeito da maturação e temperatura na germinação de sementes de *Phoenix* canariensis hort. ex Chabaud - Arecaceae. Revista Árvore 34, 31–38.
- Pritchard, H.W., Wood, C.B., Hodges, S., Vautier, H.J. (2004). 100-seed test for desiccation tolerance and germination: a case study on eight tropical palm species. Seed Science and Technology 32, 393-403.
- Reid, S., Armesto, J.J. (2011). Avian gut-passage effects on seed germination of shrubland species in Mediterranean central Chile. *Plant Ecology* **212**, 1–10
- Rey, P.J., Gutierrez, J.E. (1996). Pecking of olives by frugivorous birds: a shift in feeding behaviour to overcome gape limitation. *Journal of Avian Biology* 27, 327-333.
- Richardson, F.J., Richardson, R.G., Shepherd, R.C.H. (2006). Weeds of the south-east: an identification guide for Australia. R.G. and F.J Richardson: Meredith, Vic.
- Richardson, F.J., Richardson, R.G., Shepherd, R.C.H. (2011). Weeds of the south-east: an identification guide for Australia. R.G. and F.J Richardson: Meredith, Vic.
- Richardson, J.T.E. (2011). The analysis of 2 x 2 contingency tables Yet again. *Statistics in Medicine* **30**, 890.
- Rico-Guzmán, E., Terrones, B., Cantó, J.L., Bonet, A. (2012). Frugivore carnivores: preferences and contribution to seed dispersal of red fox Vulpes vulpes (Linnaeus, 1758) and stone marten Martes foina (Erxleben, 1777) in Carrascal de la Font Roja Natural Park (Alicante, Spain). Galemys 24, 25-33.
- Robinson, M.L. (2009). Cooperative Extension SP-02-09: Cultivated Palm Seed Germination. Reno: University of Nevada.

- Rodriguez-Perez, J., Riera, N., Traveset, A. (2005). Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and controlled conditions. *Functional Ecology* **19**, 699-706.
- Ryszkowski, L., Wagner, C.K., Goszczyński, J., Truszkowski, J. (1971). Operations of predators in a forest and cultivated fields. *Annales Zoologici Fennici* 8, 160–168.
- Saro, I., Robledo-Arnuncio, J.J., González-Pérez, M.A., Sosa, P.A. (2014). Patterns of pollen dispersal in a small population of the Canarian endemic palm (*Phoenix canariensis*). Heredity 113, 215-223.
- Schmelitschek, E., French, K., Parry-Jones, K. (2009). Fruit availability and utilisation by grey-headed flying foxes (Pteropodidae: Pteropus poliocephalus) in a human-modified environment on the south coast of New South Wales, Australia. Wildlife Research 36, 592–600.
- Sequeira, D.M. (1980). Comparison of the diet of the red fox (Vulpes vulpes L., 1758) in Gelderland (Holland), Denmark and Finnish Lapland. In: Zimen E, ed. *The Red Fox*. Dordrecht: Springer. 35-51.
- Silverstein, R.P. (2005). Germination of native and exotic plant seeds dispersed by Coyotes (*Canis Latrans*) in Southern California. *The Southwestern Naturalist* 50, 472–478.
- Singh, R.S., Bhargava, R. (2009). Effect Of Seed Treatments on Germination and Growth Behaviour in Date Palm (Phoenix Species) under hot arid Conditions. *Journal of Tropical Forestry* 25, 42-48.
- Sosa, P.A., Naranjo, A., Márquez, M., Gil, J., Saro, I. (Year) of Conference. Mapping of palm trees and palm groves (*Phoenix canariensis*) from the Canary Islands: Distribution and census. EUNOPS XVI. International Meeting of the European Network of Palm Scientists. Las Palmas de Gran Canaria.
- Spanner, T.W. (2018). Phoenix canariensis. Canary Island Date Palm. München: Rare Palm Seeds.
- Spennemann, D.H.R. (2018a). Canary Islands Palms (*Phoenix canariensis*) in Australia: introduction and early dispersal. *Palms* **62**, 185–201.
- Spennemann, D.H.R. (2018b). Geographical distribution of four key ornamental and production palm species *Phoenix canariensis, P. dactylifera, Washingtonia filifera* and *W. robusta*. Albury, NSW: Institute for Land, Water and Society, Charles Sturt University.
- Spennemann, D.H.R. (2018c). Nineteenth Century Depictions of the Canary Islands Date Palm (Phoenix Canariensis). A Visual Dataset *Institute for Land*, *Water and Society Report*. Albury, NSW: Institute for Land, Water and Society, Charles Sturt University.
- Spennemann, D.H.R. (2018d). Observations on the consumption and dispersal of *Phoenix canariensis* drupes by the Grey-headed flying fox (*Pteropus polio cephalus*). *European Journal of Ecology* **4**, 41–49.
- Spennemann, D.H.R. (2018e). Phoenix canariensis seed encountered in scats and ejecta collected at Alma Park. Albury, NSW: Institute for Land, Water and Society, Charles Sturt University.

- Spennemann, D.H.R. (2018f). Review of the vertebratemediated dispersal of the Date Palm, *Phoenix* dactylifera. Zoology in the Middle East **64**, 283-296.
- Spennemann, D.H.R. (2018g). Washingtonia robusta (Mexican Fan Palm) as a coloniser in an artificial wetland at Albury, New South Wales. Cunninghamia 18, 109-122.
- Spennemann, D.H.R. (2019a). Biology, ecology and distribution of the date stone beetle, *Coccotrypes* dactyliperda (Scolytinae, Coleoptera). Zoology in the Middle East 65, 163-182.
- Spennemann, D.H.R. (2019b). Canary Islands Palms (*Phoenix canariensis*) as ornamental plants. The first thirty years of the horticultural trade. *Huntia* 17, 79–102.
- Spennemann, D.H.R. (2019c). The connective potential of vertebrate vectors responsible for the dispersal of the Canary Island date palm (*Phoenix canariensis*). Flora 259, 151468.
- Spennemann, D.H.R. (2019d). The contribution of the Canary Island date palm (*Phoenix canariensis*) to the winter diet of frugivores in novel ecosystems. *European Journal of Ecology* **5**, 11–21.
- Spennemann, D.H.R. (in press). Infestation of vertebrate defecated palm seeds by *Coccotrypes dactyliperda* (Coleoptera, Curculionidae, Scolytinae) and its implications on the dispersal of palms. *Oriental Insects*, [accepted].
- Spennemann, D.H.R., Allen, L.R. (2000). Feral olives (Olea europaea) as a future woody weeds in Australia. Australian Journal of Experimental Agriculture 40, 889–901.
- Spennemann, D.H.R., Kent, K., Cook, R. (2018). Uninvited guests: Mass Emergence of Scolytinid Beetles in a Seed Germination Experiment and its Management *Institute for Land, Water and Society Report*. Albury, NSW: Institute for Land, Water and Society, Charles Sturt University.
- Sumianah, G.M., Makki, Y.M., Rumney, T.G. (1984). Changes in the chemical composition of three cultivars of date seed during germination. *Date Palm Journal* 3, 395–407.
- Szuman, J., Skrzydlewski, A. (1962). Über die Durchgangszeit des Futters durch den Magen-Darm-Kanal beim Blaufuchs. Archiv für Tierernährung 12, 1–4.
- Traba, J., Sagrario, A., Herranz, J., Clamagirand, M.C. (2006). Red fox (Vulpes vulpes L.) favour seed dispersal, germination and seedling survival of Mediterranean hackberry (Celtis australis L.) Acta Oecologica 30, 39–45.
- Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant ecology, evolution and systematics* 1, 151-190.
- Tsuji, Y., Morimoto, M., Matsubayashi, K. (2009). Effects of the physical characteristics of seeds on gastrointestinal passage time in captive Japanese macaques. *Journal of Zoology* 280, 171-176.

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- Varela, O., Bucher, E.H. (2006). Passage time, viability, and germination of seeds ingested by foxes. *Journal* of Arid Environments 67, 566-578.
- Wheelwright, N.T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology* **66**, 808-818.
- White, J.G., Gubiani, R., Smallman, N., Snell, K., Morton, A. (2006). Home range, habitat selection and diet of foxes (Vulpes vulpes) in a semi-urban riparian environment. *Wildlife Research* **33**, 175-180.
- Zona, S. (2008). The horticultural history of the Canary Island Date Palm (Phoenix canariensis). *Garden History* **36**, 301–308.
- Zona, S., Henderson, A. (1989). A review of animal-mediated seed dispersal of palms. *Selbyana* 11, 6–21.